Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales

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Cultural processes occur in a wide variety of animal taxa, from insects to cetaceans. The songs of humpback whales are one of the most striking examples of the transmission of a cultural trait and social learning in any nonhuman animal. To understand how songs are learned, we investigate rare cases of song hybridization, where parts of an existing song are spliced with a new one, likely before an individual totally adopts the new song. Song unit sequences were extracted from over 9,300 phrases recorded during two song revolutions across the South Pacific Ocean, allowing fine-scale analysis of composition and sequencing. In hybrid songs the current and new songs were spliced together in two specific ways: (*i*) singers placed a single hybrid phrase, in which content from both songs were combined, between the two song types when transitioning from one to the other, and/or (*ii*) singers spliced complete themes from the revolutionary song into the current song. Sequence analysis indicated that both processes were governed by structural similarity rules. Hybrid phrases or theme substitutions occurred at points in the songs where both songs contained "similar sounds arranged in a similar pattern." Songs appear to be learned as segments (themes/phrase types), akin to birdsong and human language acquisition, and these can be combined in predictable ways if the underlying structural pattern is similar. These snapshots of song change provide insights into the mechanisms underlying song learning in humpback whales, and comparative perspectives on the evolution of human language and culture.

vocal learning | cultural transmission | song | cetacean | humpback whale

Cultural transmission has been shown in a wide variety of taxa, spanning birds, fish, insects, cetaceans, and nonhuman primates (1, 2). We define culture in the broad sense as shared information or behavior acquired through some form of social learning from conspecifics (3–5). Each of these studies has provided examples demonstrating a behavioral trait being passed from one individual to another, and on occasion entire populations, through some form of social learning. Cetaceans show some of the most sophisticated and complex vocal and cultural behavior outside of humans (6, 7), including vocal learning, shared traditions, and gene–culture coevolution. For example, southern right whales (*Eubalaena australis*) demonstrate strong migratory culture (8), whereas bottlenose dolphins (*Tursiops truncatus* and *Tursiops aduncus*) demonstrate the cultural transmission of tool use (9, 10). Both sperm whales (*Physeter macrocephalus*) and killer whales (*Orcinus orca*) have culturally transmitted group vocalizations that are maintained over decades (11, 12), and also appear to undergo gene–culture coevolution (13–15).

Humpback whales (*Megaptera novaeangliae*) possess multiple, independently evolving cultural traditions, including maternally directed site fidelity to breeding and feeding grounds (16), socially learned feeding tactics (17), and song displays that are subject to cultural evolution and revolution (18–20). Humpback whale song is one of the most elaborate acoustic displays in the animal kingdom (21). The song is produced solely by adult males (22) and is therefore considered a product of sexual selection, even though the details of how it functions as a signal are still debated (23).

Song is organized in a nested hierarchy: single sounds are termed "units," a sequence of units is grouped into a "phrase," phrases are repeated to form a "theme," and a number of different themes are usually sung in a set order to form the "song" (24). To move from one theme into another, a single "transitional phrase" is sometimes sung that contains content from the preceding and following themes (20). Different versions of the display (containing different themes) are termed "song types" (18). Within each population, there is usually strong conformity to a single song type at any point in time (25). However, the song is constantly changing (20), and all males must continuously incorporate these alterations to maintain the observed conformity. This slow and gradual change is a process of cultural evolution in which subtle changes occur over time at a population scale (20, 26).

Populations within an ocean basin sing similar songs, but the similarity depends on both geographic (27, 28) and temporal distances, as transmission of song changes across a region may take several years (18, 29, 30). In the western and central South Pacific region, song also undergoes dramatic cultural "revolutions," where the song type from a neighboring population is rapidly adopted by all of the males in an adjacent population (18, 19). We have previously described the rapid, repeated, and regular horizontal cultural transmission of multiple song types, creating multiple song revolutions across the western and central South Pacific region (18, 29, 30). Among populations in any nonhuman animal, this is a very rare, possibly unique, example of population-wide horizontal cultural transmission where behavioral variants are transmitted rapidly and repeatedly (18). However, we know little regarding the underlying vocal and sequence learning mechanisms governing this extraordinary cultural phenomenon.

Mechanisms of vocal learning are far better understood for human language acquisition and birdsong than for cetacean

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vocalizations (7). Humpback whales are "vocal production learners," as they are able to modify the form of their own vocal signals after experience with signals from other individuals (7). Vocal production learning is not widespread; thus far, only a few mammalian groups, including cetaceans, pinnipeds, bats, elephants, and humans have been shown to be capable of it (7). An important limitation when studying large cetacean species is the inability to conduct controlled laboratory experiments. Although learning and song production can be mapped to different pathways in the brain for songbirds, mice, and humans (to name a few) (31), this is not yet possible with large, free-roaming cetaceans. However, we can explore the learning mechanisms involved by examining the structure and arrangement of the song displays in detail, and comparing any rules we uncover governing the arrangement and learning of song to those currently known in human language acquisition and birdsong learning.

Statistical learning, where patterns and structure are identified based on the statistical information present in sensory stimuli, is a common human learning mechanism present in all sensory modalities (32). From a very young age human infants are able to detect, extract, and generalize statistical regularities (i.e., simple algebraic rules) from their auditory environment (32, 33), and understanding how they use this statistical information to learn language is a major research focus (32). The ability to detect transition probabilities—the probability that a given sound or syllable follows another one (32, 33)—is important in understanding word segmentation or grammar learning tasks. From a comparative perspective, recent work has demonstrated that zebra finches (*Taeniopygia guttata*) generate phonological categories that result in the song being easier for others to learn (34). Understanding how humpback whales learn their extended song sequences is therefore of interest in the comparative study of mechanisms for learning sequences and patterns in cultural vocal signals.

Segmentation, the chunking of sequences into smaller components (phrases or words) that can later be recombined, is another important mechanism in human language acquisition (32, 33, 35, 36). Songbirds have been shown to segment when learning their song displays (37–40). Segments are typically separated by longer pauses (silence), and these pauses may provide an emphasis that aids in memorization of segment chunks (39). In a recent review of human language and nonhuman animal communication, Birchenall (33) suggests that the process of segmentation may also be present in humpback whale song learning. Given the importance of segmentation to language acquisition and the presence of this mechanism in the learning of birdsong, this is a logical starting place to study humpback whale song learning.

Here, we present evidence that humpback whales use segmentation in song learning by examining recordings made during the process of learning a new song in the context of a song revolution event. Recording a whale in the act of changing his song is challenging; they are highly mobile and one cannot simply record all of an individual's song during a 2- to 3-mo breeding season and >6,000-km migration. We therefore investigate some rare cases of song hybridization recorded during song revolution events to understand how individual whales transition between two different songs. These hybrid songs, which contain themes and elements from both the previous song and the new, revolutionary song, presumably represent a transition phase in the process by which singers change their song display to a new, completely different arrangement. We aim to identify if there are any underlying structural rules governing song change (e.g., segmentation, transition probabilities) that can provide insight into how new songs can be learned so rapidly. We hypothesize that new songs will be learned as segments if segmentation is a taxon-general mechanism (hypothesis 1). Identifying the level in the song hierarchy (phrase, theme, or song) that comprises a segment will provide important information as to how the song is memorized. Alternatively, parts of both song types may be spliced together in a random arrangement of new and old units. This would indicate that the structural arrangement of an individual's song disintegrates to a babbling/subsong phase (41) before learning the new song arrangement, and that segmentation is not occurring. Additionally, we hypothesize that if segmentation occurs, then the combination of these segments from both song types by an individual will not be random (hypothesis 2). That is, the insertion of new song segments into the existing song will be at locations in the existing song where there is some structural similarity in the sound units, phrases, or themes of the old and new songs, rather than at random positions. This "similar sounds in similar arrangements" mechanism would be akin to word substitutions in humans, such as malapropisms, where an incorrect word with a similar sound is used in place of the correct word (42). To test these hypotheses, we first investigated how each singer displaying a hybrid song transitioned between song types, and second we quantified the similarity in arrangement between the themes from each song using sequence analysis metrics. We analyzed four hybrid songs recorded during two different song revolutions from two geographic locations (eastern Australia and French Polynesia). Thus far, these are the only examples of hybrid songs in over 20 y of fieldwork from five populations where song revolutions are known to occur regularly, and from which ∼1,500 song sequences representing at least 100,000 phrases have been analyzed. [A fifth hybrid song has been identified. This recording is of a very poor quality (low signal-to-noise ratio). Themes can be sporadically identified but the clear transitions between themes required for the current analysis is lacking. We therefore excluded this recording from analysis. The recording was from eastern Australia in 1997 as part of the pink/black song revolution presented in ref. 19.]

Results

Three separate datasets were included in the analysis, as each contained one or more hybrid songs. These spanned two geographic locations: Peregian Beach, eastern Australia (1996–1997 and 2002–2003), and Mo'orea, French Polynesia (2005); and two song revolutions: from pink to black (Australia 1996–1997), the "original" song revolution (19), and from blue to dark red [which occurred in Australia in 2002–2003 and French Polynesia in 2005 (20)]. Over 46 h of song from 50 singers and 4 song types (each given an arbitrary color label—blue, dark red, pink, and black—to be consistent with published analyses of these song types) were analyzed from French Polynesia (2005: 18 singers, 1 hybrid) and eastern Australia (1996–1997: 2 singers each based on the highest quality singer for each song type from 249 singers presented in ref. 19, 2 hybrids; and 2002–2003: 26 singers, 1 hybrid).

To identify if new songs were learned as segments (hypothesis 1), we first needed to classify each potential segment. Because there are multiple levels in the humpback song hierarchy, each being a potential basis for segmentation, we analyzed each level. First, individual sounds were classified into categories (i.e., unit types) (*SI Methods* and Tables S1 and S2). Then the stereotyped sequences of units that made phrases were established and further grouped into themes (*SI Methods* and Table S1). Themes from each song type were labeled 1 through 37 (Table 1; also see *SI Methods* and Table S1) following previous classification of these song types (18, 19, 29, 43, 44). The song type of origin (pink or black) for theme 11 was uncertain and thus remained unresolved, as it was not heard in any nonhybrid songs (Fig. 1, Table 1, and Table S1). The sequence of themes for each hybrid singer was established (Table 1). It is immediately obvious that the hybrid songs examined here comprised complete themes from the two different song types combined into a single song; segmentation occurred at the theme level.

Table 1. Theme sequence of hybrid songs from French Polynesia (2005) and eastern Australia (1997 and 2003)

Song types	Location/year	Singer (date)	Recording length h:min:s	Theme sequence
Blue (old) and dark red (new)	French Polynesia 2005	HYB1 August 31	0:14:25	24, 26*b*, 27, 28*a*, 29/24, 24, 24/37*a*, 37*a*, 37*b*, 37*a*, 37*a*/31*a*, 31*a*, 31*b*, 33, 34, 36, SLA, 25*a*
	Eastern Australia 2003	HYB2 September 26	1:37:58	25*a*, 25*b*, 27/31*a*, 31*a*, 31*b*, cont.*, 31*b*, 31*a*, 31*a*/27, 27, 27/31*a*, 31*a*, 31*b*, cont.*
Pink (old) and black (new)	Eastern Australia 1997	HYB3 July 20	1:29:09	8*a*, 9*b*, 8*a*, 11, 8*a*, 8*b*, 9*b*, 8*a*, 9*b*, cont.†, 8*b*, 9*b*, 9*b*/4, 4, SLA, 5*a*, 5*b*, 1, 11, 8*a*, 9*b*, cont.†, 8*b*, 8*a*, 9*b*, cont.†, 9*b*/4, SLA, 5*a*, 5*b*, 1, 1/7*b*, 7*b*, 7*b*/8*a*, 9*b*, 8*a*, 9*b*, cont.†, 8*a*, 9*b*, 8*a*/5*b*, 5*a*, 5*b*, 1, 1/7*b*, 7*b*, 8*a*, 9*b*, cont.†, 9*b*/4, 4, 5*a*, SLA, 5*a*, 5*b*, 1, 1/7*b*, 7*b*, 8*a*, 9*b*, cont.†, 9*b*/4, 4, 5*a*, 5*b*, 1, 1/7*b*, 7*b*, 8*a*, 9*b*, cont.†, 9*b*/4, SLA, 5*a*, 5*b*, 1, 1/7*b*, SLA
		HYB4 September 4	3:22:42	9*b*, 8*b*, 9*b*, 9*b*/4, 4, SLA, 10*a*, SLA, 10*a*, 1, 1/7*b*, 7*b*, 7*b*/11, 11, 11/8*b*, 8*b*, 9*b*, cont.‡, 9*b*/4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 8*b*, 9*b*, 9*b*/4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 9*b*, 8*b*, 9*b*/4, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, cont.‡, 4, SLA, 10*a*, 5*b*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 8*b*, 9*b*, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, cont.‡, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 8*b*, 9*b*, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 8*b*, 9*b*, 8*b*, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 8*b*, 9*b*, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 8*b*, 9*b*, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, cont.‡, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, 11, 11/8*b*, 8*b*,
			0:41:02	9*b*, 8b, 9*b* // 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, SLA, 5*b*, 1, 1/7*b*, 7*b*, 11, 8*b*, 9*b*, 4, 10*a*, 1, 1/7*b*, 7*b*, 11, 11/8*b*, 8*b*, 9*b*, 4, SLA, 10*a*, 1, 1/7*b*, 7*b*, SLA, 7*b*

/ Represents a transitional phrase between the two labeled themes. // Represents a break in recording for <1 min. SLA, surface level attenuation, where the whale is breathing at the surface and the song content is difficult to hear and therefore uncertain. Themes are color-coded by song type. Note the song type of origin for theme 11 was uncertain (colored gray). See Table S1 for description of theme content.

*Themes 31*a* and 31*b* repeated multiple times. No break in recording.

†Themes 8*a* and 9*b* repeated multiple times. No break in recording.

‡Themes 8*b* and 9*b* repeated multiple times. No break in recording.

Given that hybrid songs contained theme segments from each song type, we investigated if there were any patterns to the arrangement of themes (hypothesis 2). To do this, we: (*i*) established the location of hybrid transitions in the song, (*ii*) investigated how each singer transitioned between the song types, and (*iii*) quantified the similarity of theme content using sequence analysis metrics to understand why a singer might switch at that particular location in the song.

To understand the location of theme transitions, the full sequence of themes from all singers was used to construct a first-order Markov model based on the frequencies of transition between phrases (Fig. 2). Transitions occurred between the pink and black song types at multiple locations in the song (Fig. 2*A* and Table 1) but, in contrast, transitions between the blue and dark red song types occurred only at two locations in the song (Fig. 1 and Fig. 2*B*). At these transition locations, singers often placed a transitional phrase between the two song types to mediate the transition (Tables 1 and 2). This single phrase combined the starting units from the preceding phrase with units from the following phrase (typically the ending units) (Fig. 1, Table 2, and Table S1).

We characterized the structural similarity, that is the similarity in the sequence of units that comprised each theme/phrase type (laid out in Table S1), between each pair of songs (e.g., blue vs. dark red) using the Levenshtein distance (LD), a common similarity metric in linguistic and humpback song comparisons (29, 43, 45, 46). In songs from the 2005 French Polynesia blue/dark red revolution, hierarchical clustering of themes showed a single location on the dendrogram where themes from both song types grouped together on a branch (Fig. 3*A*). This was where the singer of the hybrid song in the French Polynesian dataset switched between song types (Fig. 2 and Tables 1 and 2). In songs from the eastern Australia 2002 revolution involving the same song types, this pattern was not as clear because theme transitions did not occur at the most similar themes (Fig. 3*B*). Instead, theme transitions were mediated by a transitional phrase (Tables 1 and 2). Finally, in songs from the 1996 eastern Australia pink/black revolution, the dendrogram showed a single location where themes from both song types grouped together on a branch (Fig. 3*C* and *SI Results*). This was where the majority of transitions in hybrid songs occurred between the song types (Table 2). The hybrid singers replaced the next theme in the song sequence with a similarly arranged theme from the other song type (Fig. 1 and Table 2). The remaining theme transitions were either mediated by a transitional phrase or the mechanism of transition between the song types was unclear (Tables 1 and 2). Regardless, in addition to transitional phrases this final analysis strongly indicates that transitions between song types are not random and occur more often at locations where theme content is most similar.

Discussion

Hybrid songs are recorded extremely rarely but are of interest because they capture some part of the process by which singers change their song display from an older version (type) to a new, completely different arrangement. The hybrid songs presented here were all captured during song revolution events, when singers using both the old and new song types were in the same population. It is clear that new songs are learned as segments, confirming hypothesis 1 (see also ref. 33), indicating that segmentation is a learning mechanism found in the cetacean lineage. The way singers move between song types during singing

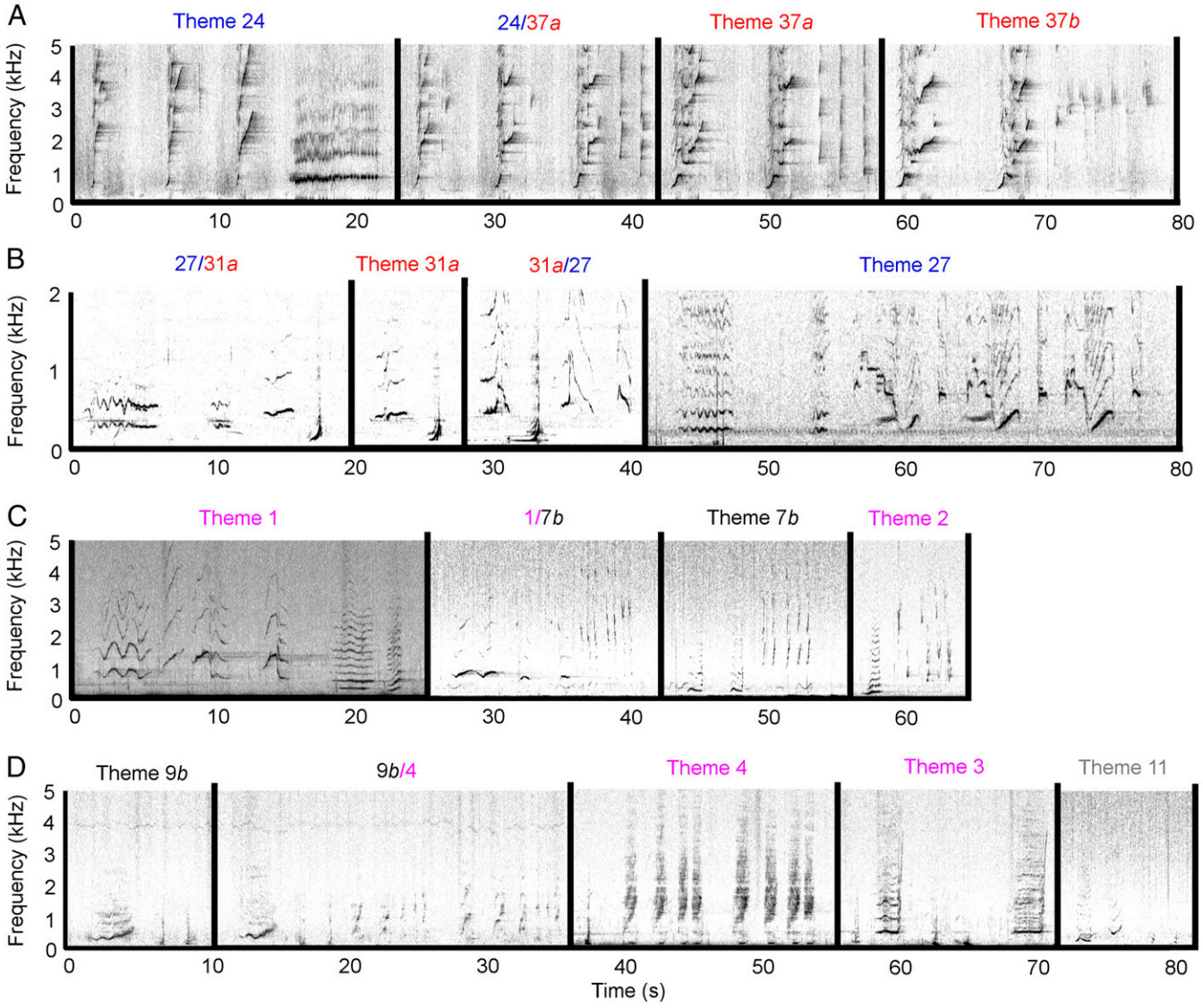

Fig. 1. Example spectrograms of hybrid transitional phrases, corresponding parent themes, and substituted themes from the blue and dark red song types (*A* and *B*), and the pink and black song types (*C* and *D*). *A* shows the theme progression (from left to right) of the transition from blue theme 24, through the hybrid 24/37*a* phrase into dark red theme 37*a* and then theme 37*b* (singer HYB1) (Table 1). *B* shows the theme progression from dark red theme 31*a* to blue theme 27, mediated by hybrid transition phrases 27/31*a* and 31*a*/27 [note the difference in arrangement depending on the direction of transition (singer HYB2)]. *C* shows the theme progression (from left to right) from pink theme 1, through hybrid phrase 1/7*a* into black theme 7*a* (singers HYB3 and HYB4) (Table 1), and the substituted pink theme 2. *D* shows the theme progression (from left to right) from black theme 9*b*, through hybrid phrase 9*b*/4 into pink theme 4 (singers HYB3 and HYB4) (Table 1). It also shows pink theme 3 and the unresolved theme 11. Spectrograms were 2,048-point fast Fourier transform (FFT), Hanning window and 75% overlap, generated in RAVEN PRO 1.4 (see also Audios S1–S4 for corresponding audio files).

bouts suggests that these displays are unlikely to be learned as a whole. Instead, songs are split into theme segments, and the fact that transitions between song types occur at specific points in the theme sequence suggests that each theme is learned as a separate entity. Segmentation or chunking of sequences is an important mechanism in human language acquisition (35), where a stream of utterances is segmented into smaller components (phrases or words) and later recombined (36). Songbirds have also been shown to segment their song displays (37–40) and statistically learn sound categories (34). Juvenile male songbirds may learn their song from one or more tutors as a sequence of syllable segments, which they recombine to form their own song (37–40). In humpback whales, our results suggest that a male learns the new song as theme segments, which he combines with older themes as he progressively learns the new song. The novelty-threshold hypothesis suggests that novelties in the song are adopted by singers once reaching a threshold prevalence (47), and therefore an individual male would need to hear a new song from multiple individuals before adopting the change. The male therefore has multiple potential models for each theme and a general overview of the "correct" sequence of the themes. The highly stereotyped nature of theme and phrase sequences, both of which we quantified as transition probabilities (e.g., Fig. 2 and ref. 48), strongly suggests humpback whales, like songbirds, use statistical learning in learning their song display (34).

In songbirds, segments are typically separated by longer pauses (silence), and these pauses may provide an emphasis that aids in memorization of segment chunks (39). This feature of pauses between segments of zebra finch song is also a feature of humpback whale song, as a phrase is delineated from the start of another phrase by a longer pause (24, 49). Given that a single

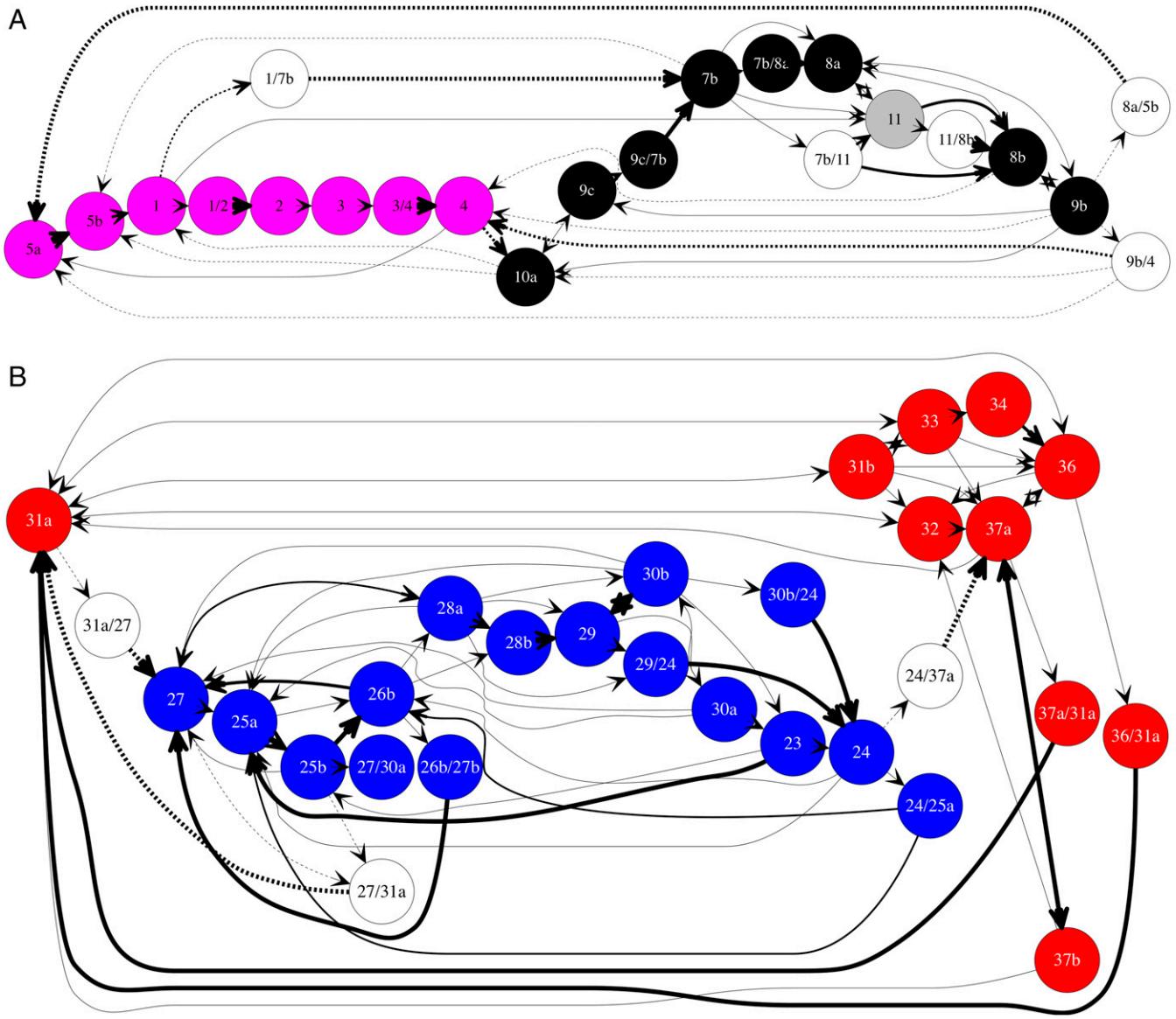

Fig. 2. First-order Markov model of theme transitions to understand hybridization between (*A*) pink/black song types (n = 2,222 phrase transitions, n = 4 individuals), and (*B*) blue/dark red song types (n = 8,852 phrase transitions, n = 46 individuals). Each node represents a theme or phrase type, color-coded by song type. White nodes represent transitional phrases and dashed lines indicate transitions between song types. Arrows represent the direction of movement and thicker lines indicate higher transition probabilities. Transitions between the pink and black song types (*A*) occurred at multiple locations (themes 1 to 7*b*, 9*b* to 4, 10*a* to 1, 4 to 10*a*, 10*a* to 5*b*, 8*b* to 4, and 8*a* to 5*b*). In contrast, transitions between the blue and dark red song types (*B*) occurred only at two specific locations in the song: blue theme 27–dark red theme 31*a* (both directions), and blue theme 24–dark red theme 37*a* (one-way). Phrase repetitions are removed from the figure for ease of display.

humpback whale song can last anywhere from 5 to 30 min (24), any aid in memorization of such a long display would be under strong selection. The repetition of phrases within themes introduces redundancy in the song, and likely aids memorization through repetition and reduced content. Furthermore, rhyme-like patterns in humpback song (50) appear similar to rhyme patterns in human poems or prose, which also aid recall (51). The question of how humpback whales remember their song display (they rarely sing the wrong thing) is still open. From playback studies we know humpback whales react more strongly to novel songs than to the song of the current year (see ref. 52). The whales can identify "same" from "different." It would be interesting to explore how long their song memory lasts, as bottlenose dolphins have been shown to remember vocalizations (signature whistles of conspecifics) for over 20 y (53). Such a song memory could drive the directional change in song revolutions (to stop whales reverting back to the previous song type), leading to the broad-scale cultural phenomenon we observe (18).

Hybrid songs from both song revolutions contained themes from one song type that were spliced into the middle of the other song type (Table 1). There are multiple examples of such hybrid song production in songbirds at the boundary of two song dialect areas or the boundary between two closely related species (41). For example, orange-tufted sunbirds (*Nectarinia osea*) have sharp dialect boundaries, but a small number of birds along these boundaries sing songs from both dialects (i.e., hybrids) (54). Similarly, in the village indigobird (*Vidua chalybeata*), a species that undergoes continuous population-wide song evolution in some ways similar to humpback whale songs, males along dialect boundaries have been recorded singing hybrid songs that combined songs from each

Table 2. Theme transitions between two different song types in hybrid songs

Theme transition	Direction transition	%	Supported by dendrogram?	Similarity in units/arrangement	Transitional phrase present?	Description
24 to 37*a*	Old→new	33 (1/3)	Yes (24 and 37*a*) Partial (24 and 37*b*)	Two starting units are highly similar	Yes (24/37*a*) Starting units theme 24, then ending units theme 37*a*	Similarity and transitional phrase
27 to 31*a*	Old→new	33 (1/3)	No	None	Yes (27/31*a*) Starting units (2) from theme 27, then theme 31*a*	Transitional phrase
31*a* to 27	New→old	33 (1/3)	No	None	Yes (31*a*/27) Theme 31*a*, then ending units (2) from theme 27	Transitional phrase
1 to 7*b*	Old→new	38 (21/56)	No (1 and 7*b*) Yes (2 and 7*b*)	Most units of theme 2 and 7*b* are highly similar, appears to replace next theme in sequence with similar theme	Yes (1/7*b*) Starting units (2) from theme 1, then ending units from theme 7*b*	Similarity and transitional phrase
9*b* to 4	New→old	30 (17/56)	No	One shared unit type	Yes (9*b*/4) Starting unit from theme 9*b*, shared unit, then ending units from theme 4	Transitional phrase
10*a* to 1	New→old	25 (14/56)	No	None	No	Unclear
4 to 10*a*	Old→new	2 (1/56)	No	None	No	Unclear
10*a* to 5*b*	New→old	2 (1/56)	No	None	No	Unclear
8*b* to 4	New→old	2 (1/56)	No	None	No	Unclear
8*a* to 5*b*	New→old	2 (1/56)	No	None	Yes (8*a*/5*b*) Theme 8*a* and two units from theme 5*b*	Transitional phrase

The direction of transition (i.e., old song to new song, or vice versa), and the number of times this transition occurred as a percentage of the total number of hybrid transitions for each pair of song types (taken from Table 1) are noted. The similarity in sound units or their arrangement is described along with whether this similarity was supported in the dendrograms (i.e., both themes present on a branch). The presence of a transitional phrase is noted, and a description of the potential mechanism assisting the transition is suggested.

dialect (55). In yellow-rumped caciques (*Cacicus cela vitellinus*), another species with continuous population-wide song evolution, males in a colony may occasionally incorporate a foreign song type as part of their yearly population dialect if the two colonies are closely situated (56). In another example, at the range interface of black-capped chickadees (*Poecile atricapillus*) and Carolina chickadees (*Poecile carolinensis*), birds from both species displayed bilingual or atypical repertoires (57). Clearly, segmentation is an important general mechanism in vocal learning present in multiple independent lineages.

Transitions between humpback whale song types were often mediated by a transitional phrase containing individual sound units from the previous and following phrases that were common to both song types (Figs. 1 and 2 and Tables 1 and 2). Transitional phrases are a neglected component of the song in general, as they are often excluded from analyses focused on delineating song types (49). The variable structure of transitional phrases can make them difficult to categorize, particularly if they are not routinely used in all transitions between themes. Nevertheless, it is clear this normal component of song organization is important to allow an ordered progression from one theme into another, regardless of the song types.

Transitions between song types were partially governed by structural similarity, based on the Markov model and sequence analysis (Figs. 2 and 3), rejecting random combinations of segments (hypothesis 2). The sequence analysis indicated that transitions or theme substitutions occurred more often in locations that contained "similar sounds arranged in a similar pattern" in old and new songs (Fig. 3). Themes either progressed into a similarly sounding theme of the other song type or replaced that similarly sounding theme altogether (Table 2). In addition to segmenting, song learning and change are partially governed by structural similarity rules where transitions or theme substitutions occur in locations that contain similar sounds arranged in a similar pattern (i.e., a "switch-when-similar" rule). Word substitutions in humans, such as malapropisms—the use of an incorrect word in place of a word with a similar sound (42)—is highly suggestive for a general mechanism. These transition points based on similarity could act as a point of reference or cue, allowing the singer to switch from the old into the new song at this position in the song. Such anchors are present in human vocal performances [e.g., oral traditions (51)], and single sounds or words and similar note arrangements are used to transition among songs in human music performances. Finally, the ability to jump from one song into another is also a feature of birdsong; for example, counter-singing allows a male to select a matching song of a rival male and switch to singing that song in an aggressive context (41). This skill strongly suggests the presence of an underlying mechanism allowing plasticity in vocal output shared among vocal learning species.

We suggest the switch-when-similar rule may be stronger and thus more important in one direction (i.e., old-to-new themes) (Table 2), assisting singers in learning new themes sequentially and in the "correct" order. The whale is attempting to learn the new display; this is very directional. The location in the song where old themes encroach back into the song display may be less important and is unlikely to be governed by this similarity rule (explaining the majority of unsimilar transitions backward). These new-to-old song transitions appear to be mediated more often by transitional phrases (Table 2).

The process of vocal production learning (7) of a completely new song type could occur through a number of structural changes to the song, as new themes must be learned and old themes removed. Multiple studies indicate that male humpback whales adhere to the current arrangement of the song (e.g., refs. 20 and 25). Importantly, once a new song is recorded in a population, all males switch to this new song (18, 19). Clearly, the song is learned as theme segments to aid in the learning of this

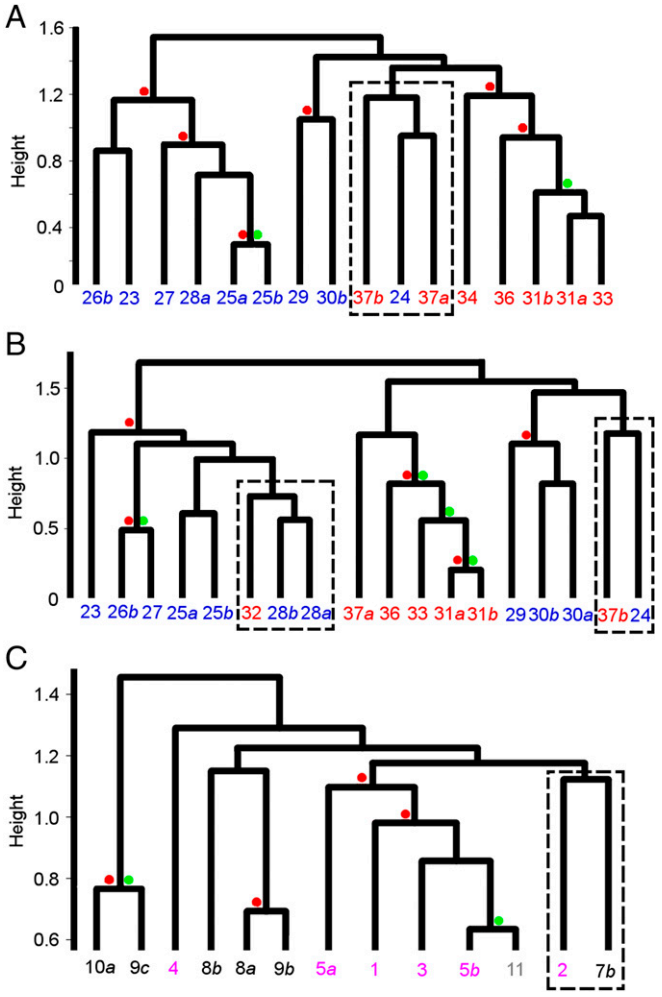

Fig. 3. Dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for (*A*) French Polynesia 2005 blue and dark red song types (CCC = 0.93), (*B*) eastern Australia 2002–2003 blue and dark red song types (CCC = 0.88), and (*C*) eastern Australia 1996–1997 pink and black song types (CCC = 0.95). Multiscale bootstrap resampling (AU, *Left*, red dot indicates $P > 95\%$) and normal bootstrap probabilities (*Right*, green dot indicates $P > 70\%$) are displayed. Branches with high AU values are strongly supported by the data. Dashed boxes indicate where themes from different song types appear together on a branch.

complex display. In male village indigobirds, immigrant males add song types from their new dialect and then drop their old, foreign song types within a year (55). We suggest humpback whales may undertake a similar process by adding in new themes starting at similar locations and then progressively deleting the old themes. Intense cultural conformity is likely influencing these vocal displays, which are in turn also driven by sexual selection. The presence of an innate template likely governs the underlying processes and rules of song learning (58), overlaid with a more flexible cultural component that governs what variant of the song display to sing, regardless of the species. The details of how songs change when there is a general conformity to a population song, and how this process interacts with sexual selection that underlies the humpback song display, are important questions for future research.

Conclusions

Humpback whales provide a unique perspective for understanding of animal culture. Their mammalian heritage also makes them particularly important to our understanding of structurally arranged vocal communication and the potential origins of human language. Here, by investigating rare cases of song hybridization, where parts of an existing song are spliced with a novel, revolutionary song, we have unearthed a number of underlying structural rules governing song change, including segmentation and transition/substitution of themes based on the similarity in sound sequences. These rules likely assist humpback whales in rapidly learning their complex and ever-changing songs, and provide insights into the evolution of human language and culture.

Methods

Song Recordings. All recordings covered the frequency range of humpback whale song (see *SI Methods* for detailed recording settings). The units in each recording were transcribed by a human classifier (E.C.G. or L.L.), and a subset of units measured for a suite of acoustic parameters to ensure consistent naming (45). As humpback whale song is highly stereotyped (24), units were grouped into phrases, phrases into themes, and themes into song types. Previous studies have identified and quantified these four song types (pink, black, blue, and dark red), the themes (labeled 1–37), and unit types within each, and their cultural transmission across the western and central South Pacific (18, 19, 29, 43, 59).

Theme Transitions to Understand Song Sequences. For each recording, the sequences of themes, including phrase repetitions, transitional phrases, and hybrid phrases, were noted. Transition tables were calculated and a first-order Markov model of phrase transition probabilities was constructed for each song revolution using these data: pink to black and blue to dark red. The 2002–2003 eastern Australian and 2005 French Polynesian data were combined, given that they represented the same song types (18, 29), and the aim of this higher-level analysis was to identify positions within a song where a singer may transition between two song types.

Structural Similarity of Themes. The LD or string edit distance is a powerful metric for comparing humpback whale song sequences, which we and others have used extensively to understand song similarity at all levels within the song hierarchy (29, 43, 45, 46, 59–61). The LD similarity index produces a measure of similarity (between 0 and 1) among multiple sequences of varying lengths, and provides an overall understanding of the similarity of all sequences (see ref. 45). Here, we compared the sequence of units (i.e., a phrase) to establish the most representative phrase for each theme based on the similarity in the sequence of units (see *SI Methods* for further information, and Table S1) (29, 43, 45, 46). These representative phrases for each theme (laid out in Table S1) were then compared between the two song types (pink vs. black or blue vs. dark red) to quantify the structural similarity among themes in an attempt to identify any underlying structural rules for the transitions highlighted in the Markov models. Similarity scores were hierarchically clustered and bootstrapped in R using the *hclust*, *pvclust*, and *pvrect* packages to ensure the resulting structure was stable and likely to occur (43, 45, 62). Branches with high bootstrap values (AU significance $P > 95\%$ and bootstrap probability significance $P > 70\%$) are strongly supported by the data, whereas lower values suggest variability in their division (45). As a further test of how well each dendrogram represented the data, the Cophenetic Correlation Coefficient (CCC) was also calculated. A CCC score of over 0.8 is considered a good representation of the associations within the data (63).

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